J. Physiol. (1963), **166**, *pp.* 168–177
With 7 text-figures
Printed in Great Britain

REFLEX REGULATION OF THE UPPER EYELIDS, WITH OBSERVATIONS ON THE ONSET OF SLEEP

BY D. W. KENNARD AND G. L. SMYTH
From the Medical Psychology Laboratory, Department of Medicine, University of Cambridge

(*Received* 27 *August* 1962)

Muscles known to contain proprioceptive sense organs generally show evidence of adjustment to externally applied length changes. Although microscopic observation has demonstrated the presence of such sensory organs in the extra-ocular muscles of many species, evidence of such regulatory function has not been obtained, despite many recorded attempts. The work of Cooper, Daniel & Whitteridge (1955) showed that there are muscle spindles and Golgi tendon organs in human extra-ocular muscles, and also, with some variation, in those of cats, goats and monkeys. However, stretching these muscles did not evoke reflex contraction in any of the cases examined (Whitteridge, 1960). Similarly the work of Brindley & Merton (1960) showed there was no evidence of functional linkage between the extra-ocular muscles of the two sides, displacement of one eye causing no alteration in the muscles of the other eye.

The muscles of the eyelids, particularly the levator palpebrae superioris of the upper eyelid in man, may be considered to be in this group of muscles. It forms in some degree a common functional and anatomical unit with the rectus superior, while the lower eyelid receives a minor insertion of the rectus inferior.

Muscles with a particular antigravity function have pronounced reflex responses to stretch. The levator muscle of the upper lid may be seen in this context, in that its action lifts the eyelid against the force of gravity. However, gravity can only have a limited effect on the upper lid, as the observations of Sewall (1933) and Walsh (1947) showed no effect on the movements of the lid in different head positions (Kennard & Smyth, 1962).

We have examined the movements of the upper eyelid of human subjects following passive stretch and found a reflex response to be present. The study of eyelid functioning is of particular interest from the point of view of a number of states of disordered behaviour, including psychopathological manifestations, in which disturbances of position and movement of the eyelids are evident. The work we have described here is part of a series of investigations of the mechanisms controlling eyelid movement.

A preliminary note of some of this work has been published (Kennard & Smyth, 1962).

METHODS

Recording. The position of the upper eyelid was recorded by means of a photo-electric low-torque transducer, attached to the lid by a light spring lever. The transducer was supported on a frame clamped to the head (Fig. 1).

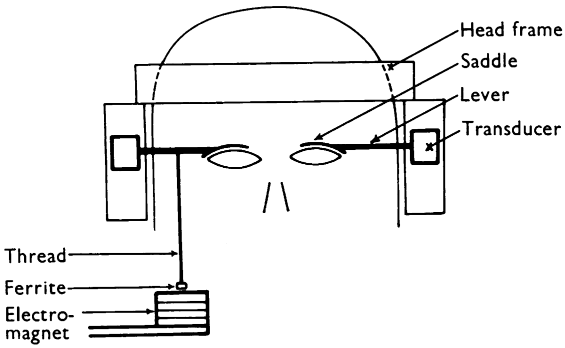

Fig. 1. Diagrammatic representation of the experimental arrangement for recording upper eyelid movement by means of a photo-electric transducer. The transducer is attached to each eyelid by means of a lever. Displacement of the right eyelid is caused by an electromagnet acting on a piece of ferrite attached to the lever by a thread.

Stretch. Displacement of the upper lid was produced by a downward force applied to the recording lever. In some experiments the force was applied by means of an electromagnet placed below the recording lever, acting on a ferrite core attached to the lever by a thread. In other experiments the force was applied by attaching a weight. For this purpose a light platform was suspended from the lever and pre-loaded as necessary, while the application was controlled by a movable support on which the platform normally rested.

Attachment to the eyelid. A small saddle of thin Perspex was stuck to the lid near the outer third so as to adhere to the skin and to a group of eyelashes. In this way a firm attachment was made, which would otherwise not be possible owing to the great mobility of the skin of the eyelid. When force was applied a more rigid form of attachment was employed, which included almost the whole of the free margin of the lid. A piece of Perspex was curved to fit the eyelid of each subject at the sulcus between the eyelashes and the eyelid. This enabled the force to be applied evenly to the whole of the lid. The recording levers were attached to these Perspex saddles both for recording and displacement.

Instrumentation. The output of the transducer was taken either in the form of a current drive for recording galvanometers of a direct-writing ultra-violet oscillograph (New Electronic Products, Ltd.) or as a voltage output to a cathode follower which was then used to drive the oscillograph.

Experimental arrangement. The subject sat in an isolated room. The head was held motionless by means of a chin rest and a support at the back of the head. During observations the subject was required to fixate a point at eye level at a distance of 1·4 m.

RESULTS

Nervous linkage between the eyelids

In order to demonstrate the phenomena described here it was necessary to record the movements of both the displaced and the contralateral eyelid simultaneously. The extra-ocular muscles show a high degree of cross-linkage, but the degree of interconnexion between the eyelids has not so far been determined. Figure 2 shows the high degree of correlation to be observed between the two lids in a subject fixating a point directly ahead.

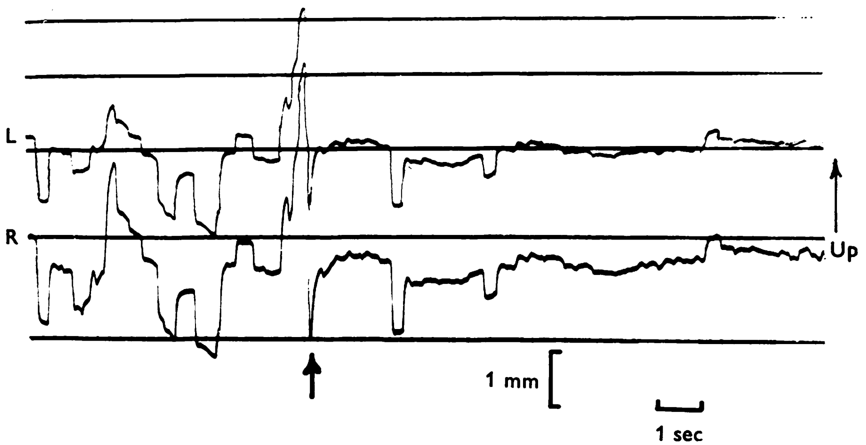

Fig. 2. Simultaneous recording from right (R) and left (L) upper eyelids. At arrow subject was asked to fixate a point at eye level. The magnification of movement (sum of eyelid position, length of lever, and electrical amplification) was adjusted to be approximately equal. A high degree of similarity and correlation is shown by the two sides with nearly all the features of one shown in the other.

All the features of the small and large movements are equally represented in each of the records. The gain of the two transducers was approximately the same, but some differences may be seen, as it is difficult to obtain identical degrees of magnification for the mechanical linkage and electrical properties simultaneously. However, the relationship between the two lids is clearly very close. The small displacements of 0·5 mm are due to saccadic movements of the eye, and in a subsequent publication details of the relation of the movements of the eyelids to those of the eyes will be described.

The neuroanatomical evidence suggests that the palpebral part of the oculomotor nucleus is a single mid-line structure, indicating that a single motor neurone pool regulates both eyelids (Duke-Elder & Wybar, 1961).

The reaction of the eyelids to maintained displacement

Sudden downward displacement was applied by means of an electromagnet whose position could be adjusted to provide displacements of various degrees. The eyelids were free to move at all times before the application of current, as the ferrite core attached to the recording lever provided negligible loading.

Reactions of displaced eyelid. The falling slope of the movement showed a break or hesitation (arrow, Fig. 3). The discontinuity appeared to be due to increased resistance offered by the eyelid.

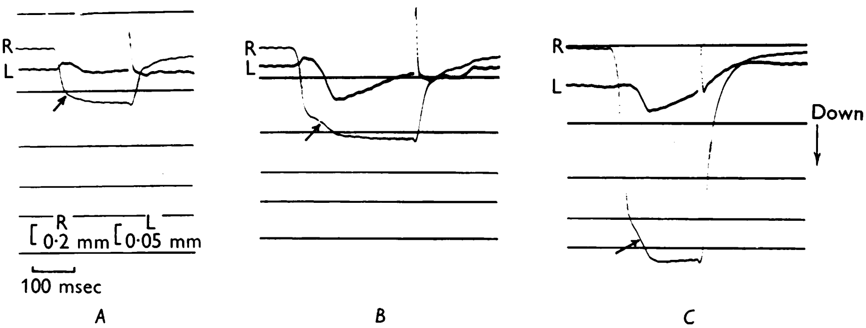

Fig. 3. Three records (A, B, C) showing the effect of sudden displacement on the right upper eyelid, and showing also the reaction of the left eyelid. The size of displacement is increased progressively from A to C. The displaced lid (R) shows increasing reaction (arrow) on the falling slope. The contralateral lid (L) shows a diphasic reaction, first upward then downward, in response to the pull. An artifact is seen in the left lid record at release of displacement (upward spike).

Small displacements of approximately 0·6 mm caused the response shown in Fig. 3A. The lid at first moved rapidly downwards, then more slowly, until within 100 msec it approximated to the lower level at which it was held by the electromagnet. With greater displacements (Fig. 3B and C) the phenomenon was progressively more marked and became a clear reaction to the stretch. It now showed as an additional 'hump' on the record. This additional wave was in a direction opposing the displacement and must have been due to a reactive contraction of the levator muscle. Consideration of the close degree of linkage between the eyelids suggested that evidence for such an action of the levator should be found on the contralateral side. Simultaneous recording on both sides confirmed that this was so.

Reactions of contralateral eyelid. Evidence of the nature of the reaction wave of the displaced lid was obtained from the contralateral lid. The contralateral lid level was raised in coincidence with the reaction seen in the displaced lid. With small displacements of approximately 0·6 mm the contralateral lid rose to a maximum of 0·04 mm and then declined to the resting level within 60 msec (Fig. 3*A*). It then declined further, going below the resting level for about 200 msec. With small displacements such downward movement was barely perceptible.

Larger applied displacements caused a more marked diphasic response. Thus displacements of 1·0 mm caused 0·6 mm rise of the contralateral lid, which after 70 msec declined to the resting level. The ensuing phase of downward movement reached a maximum value of 0·28 mm at 100 msec, and approximated to the resting level again after about 350 msec (Fig. 3*B*). The phase of downward movement increased with greater displacements, while the first phase became less evident (Fig. 3*C*).

Comparison of lid movements. To compare the reactions of the two eyelids, the reaction of the displaced lid had to be derived from the actual record, which was the sum of the imposed displacement and the reaction. The method adopted was to extend the line of the greatest slope of the record to the level finally achieved. Assuming this to be the movement which would have occurred if there had been no reaction, it was subtracted from the total recorded movement. The difference curve in Fig. 4 represents the reactive movement of the displaced lid, and can be compared directly with the movements of the contralateral lid, also shown in Fig. 4.

The timing and direction of the reaction of the two lids are similar. Both responded to downward displacement with a reaction in the opposite direction, and the peaks are coincident. Both lids then commenced to fall, the lowest point of the left lid being reached at the same time as a slowing of downward movement of the right.

Bjork & Kugelberg (1953) showed that the frequency of discharge from the levator palpebrae decreased as the gaze was lowered. This and other evidence described elsewhere (Kennard & Smyth, 1963) indicate that most movements of the upper eyelid are caused by varying activity of the levator. This suggests that the response to sudden stretch of an eyelid is a brief period of excitation of the palpebral motoneurones, followed by a longer period of inhibition. Though the levator muscles of the two sides share a common motoneurone pool, the reaction of the two sides is different, the excitatory phase on the displaced side being greater.

The reactions of the eyelids to constant loading

In contrast to the reactions to displacements of a given size, described in the previous section, we determined the reactions of the eyelids to constant force by hanging weights on the recording lever.

Downward force. The form of the response to downward application of weight, calculated from a consideration of moments acting on the lever, is shown in Fig. 5. The record shows a clear reaction where the first rapid downward movement of the weighted lid was checked, and sometimes the lid was raised slightly before it resumed the downward movement. This 'hump' or wave in the record we consider to be a similar form of response to that observed when applying constant-length displacements. Following this phase, the downward movement of the lid proceeded more slowly, but with small fluctuations superimposed. The slope of this part of the record depended on the weight, increasing with greater weights.

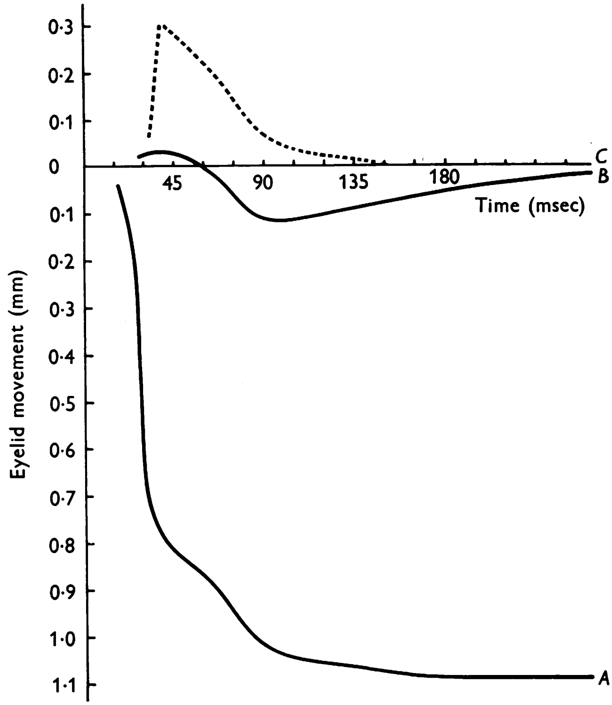

Fig. 4. The effect of sudden displacement on an eyelid. The response of the displaced eyelid, the derived reaction, and the response of the contralateral lid are shown on the same scale. *A* is the recorded curve of the displaced lid. *B* is the record of the contralateral eyelid movement. *C* is the derived curve of the displaced eyelid movement (interrupted line).

The contralateral lid showed a movement in a direction opposite to the applied force. The elevation was similar in timing to the initial reaction in the weighted lid. Thus again both eyelids showed a reaction to displacement opposing the applied force.

The prolonged decline in the position of the weighted lid resembled a lengthening reaction. It could continue for 10 sec or longer. It was probably not simply a passive muscular extension but involved inhibitory work, though it could also be a fatigue phenomenon. The contralateral lid did not show a phase of relaxation below the resting level, as described in the previous section, but the extension of the weighted lid may have continued to evoke an opposing reaction.

Upward force. Weights were applied to the eyelid over a pulley to exert upward force on the upper lid (Fig. 6). The weighted lid moved up rapidly at first, then remained stationary, but a reaction of the form seen with downward loading did not occur.

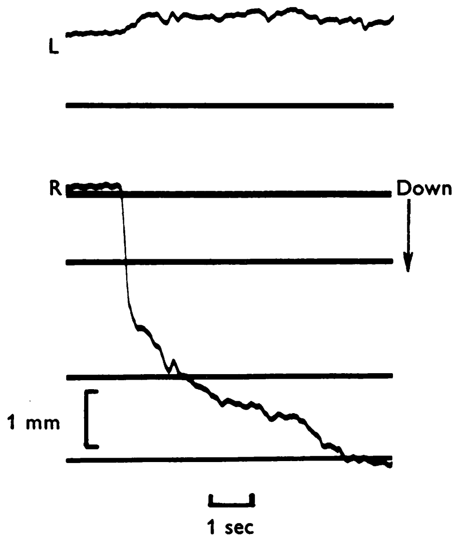

Fig. 5

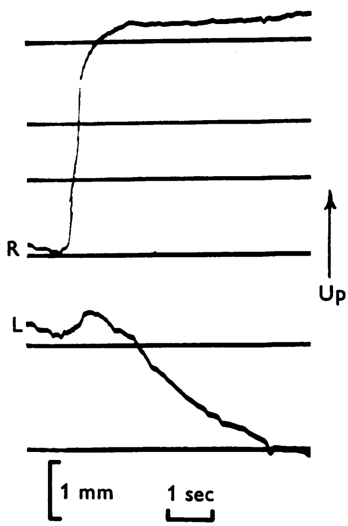

Fig. 6

Fig. 5. The reaction of the eyelids to sudden downward loading of one eyelid (right) with 2·2 g. The right lid shows a reaction in opposition to the displacement followed by a lengthening reaction. The contralateral lid shows an upward movement.

Fig. 6. The reaction of the eyelids to sudden upward loading of one eyelid (right) with 6·6 g. The right lid shows little reaction, but the contralateral lid (left) was immediately raised and then lowered approximately 2·5 mm.

The contralateral lid showed a diphasic response, with a brief movement in the direction of displacement lasting 1–4 sec followed by a prolonged decline in the level, i.e. in a direction opposite to the displacement of the weighted lid, lasting 10–20 sec. The downward movement of the contralateral lid could have been due to a relaxation of the levator muscle or to a contraction of the orbicularis. Evidence on this point is not available, but in view of the minimum participation of the orbicularis in eyelid movements other than blinks and eye closure (Gordon, 1951; Bjork & Kugelberg, 1953; Kennard & Smyth, 1962), a relaxation of the levator is the most likely cause. Upward loading of one lid relieved the normal stretch stimulus to the receptors of the levator muscle, probably reducing the activity of the palpebral motoneurone pool. This caused relaxation of both levators, but only the contralateral lid made a downward movement, as the weighted lid was held suspended.

The onset of sleep

During the observations on the reactions to downward application of weights to the upper eyelids, the opportunity arose to record the changes at the onset of sleep when subjects became drowsy. Figure 7 shows that the relaxation of the weighted lid following the application of a load was considerably increased. Following a series of records obtained during this drowsy period the subject was commanded to 'wake up'. He started and blinked several times, and it was seen that the response to weight application had considerably decreased again. The rate of fall in the wakeful

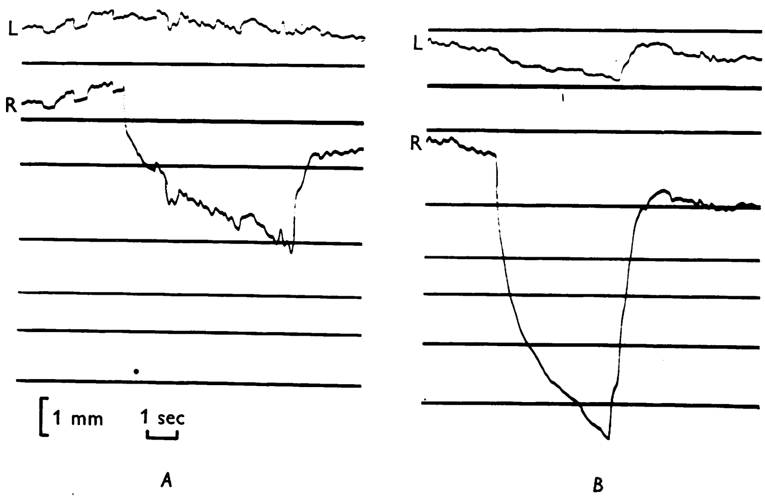

Fig. 7. The effect of drowsiness on the lengthening reaction of the upper eyelid. In both records *A* and *B* the right (R) eyelid was loaded suddenly with 2·2 g. *A* was before and *B* during drowsiness. Record *B* shows a great increase in the movement of the eyelid on loading. The contralateral lid (L) showed no reaction when wakeful, but followed the response of the displaced lid when drowsy.

state was 0·4 mm/sec for a 2·2 g weight, while during drowsiness the rate of fall caused by the same weight was 1·0 mm/sec. During drowsiness the contralateral lid was depressed slightly while the weight was applied. The phenomenon was striking enough to be observed with the naked eye.

This reaction of the eyelid may be seen to be further evidence for the reflex nature of the control of the upper eyelid. The tension and control loop sensitivity were probably decreased at the onset of sleep.

DISCUSSION

The observations showing a reflex response of the eyelids to externally applied displacement contrast with the lack of response shown by all other extra-ocular muscles that have been examined. The difference may be due to the different functions performed by the eyelids, as opposed to those of the eye. The eyelids function as a shutter, closing at the onset of sleep. There are other movements of the eyelids, such as those during blinks and accompanying vertical eye movements, which are not necessarily related to such a shutter mechanism. It is common knowledge that the eyelids follow changes in the direction of gaze, and we have examined the detailed properties of this linkage (Kennard & Smyth, unpublished observations). The connexion between the movements of the eye and the eyelid may reflect the close association between the levator palpebrae superioris and the rectus superior. In fact, the eyelids could be kept open in the wakeful state and simply closed at the onset of sleep. However, in addition, the levator palpebrae superioris fulfils an anti-gravity function and it may be also in virtue of this that a different type of control mechanism is required.

The sense organs of the extra-ocular muscles have not been demonstrated to be relevant to the reflex functioning of these muscles (Whitteridge, 1960) or to contribute to conscious eyeball position sense (Brindley & Merton, 1960). This may be related to the particular type of movement executed by the eyes and the degree of control exerted by the higher centres of the brain, where the visual system is highly represented. The eyelids are relatively unimportant components of the visual system. The cortical representation of the eyelids is small compared with that of the ocular system itself, and the degree of control necessary for the functions they perform is probably of lower order than for the muscles moving the eyeball. The eyelids do not participate in the fine discriminatory work of the visual system. A certain degree of local reflex regulation, such as that described here, may thus be seen as an example of the general pattern of nervous control of muscle, where simple reflex control is delegated to lower levels.

Sleep. Our observations are consistent with the inhibition theory of sleep. The lengthening reaction on loading the upper lid downward can be considered as an inhibition of the motor neurone responsible. Sleep caused this phase of relaxation to be very considerably increased. This reaction to applied load thus parallels the drooping of the eyelid which occurs in association with sleep.

SUMMARY

1. The upper eyelid of the human subject was passively stretched and its subsequent movements and those of the contralateral eyelid were recorded.

2. Downward stretch resulted in a brief period of increased resistance to displacement, followed by a prolonged period of progressive lengthening. Immediately after the stretch the contralateral lid briefly rose above, and then declined below, the resting level.

3. The response to upward displacement was primarily in the contralateral lid, which progressively declined below the resting level.

4. At the onset of sleep the lengthening reaction of the displaced lid was more pronounced.

5. These responses and their possible mechanisms are considered in relation to the neural control of eye and eyelid movements.

The authors would like to express their thanks to Professor D. R. Davis for his encouragement and for detailed discussion of this publication. Thanks are due to the Ford Foundation for the continued support of this work, and also to Mr Z. F. Kellerman for generous help with recording equipment.

REFERENCES

BJORK, A. & KUGELBERG, E. (1953). The electrical activity of the muscles of the eye and eyelids in various positions and during movement. *Electroenceph. clin. Neurophysiol.* **5**, 595–602.

BRINDLEY, G. S. & MERTON, P. A. (1960). The absence of position sense in the human eye. *J. Physiol.* **153**, 127–130.

COOPER, S., DANIEL, P. M. & WHITTERIDGE, D. (1955). Proprioceptors in the extrinsic eye muscles. *Brain*, **78**, 564–583.

DUKE-ELDER, S. & WYBAR, K. C. (1961). *System of Opthalmology*, Vol. 11, The anatomy of the visual system. London: Henry Kimpton.

GORDON, G. (1951). Observations upon the movements of the eyelids. *Brit. J. Ophthal.* **35**, 339–351.

KENNARD, D. W. & SMYTH, G. L. (1962). The eyelid reflex response to stretch. *Nature, Lond.*, **194**, 521–522.

KENNARD, D. W. & SMYTH, G. L. (1963). The causes of downward eyelid movement with change of gaze and the study of the physical factors concerned. *J. Physiol.* **166**, 178–190.

SEWALL, E. C. (1933). Decompression of the facial nerve. *Arch. Otolaryng., Chicago*, **18**, 746–752.

WALSH, F. B. (1947). *Clinical Neuro-Ophthalmology*, pp. 228–229. Baltimore: Williams and Wilkins.

WHITTERIDGE, D. (1960). Central control of eye movements. In *Handbook of Physiology*, ed. FIELD, J., MAGOUN, H. W. & HALL, V. E. Sect. 1, 2; pp. 1089–1109. Washington: American Physiological Society.